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A new crayfish Family (Decapoda : Astacida) from the Upper Jurassic of China, with a reinterpretation of other Chinese crayfish taxa

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Abstract. The highly sporadic fossil record of freshwater crayfish is improved by the discovery of several new specimens from the Upper Jurassic Jehol Group of Liaoning Province, north-east China. As a result of work on this material, the Family Cricoidoscelosidae is erected to accommodate specimens possessing highly atypical features among the Infraorder Astacidea belonging to the new genus and species *Cricoidoscelosus aethus*. Furthermore, *Astacus spinirostrius* Imaizumi (1938) is synonymized with *A. lincenti* van Straelen (1928b) and is moved from the Family Astacidae to the family Cambaridae and to the new genus *Palaeocambarus*. Thus, a solution is suggested to the problematic biogeographic issue of the presence of the genus *Astacus* in a region presently occupied only by cambarid crayfish, a generic assignment that was made tentatively in the first place. In addition, new questions now arise with respect to the origins and early development of crayfish in the Asiatic region and perhaps even globally.

Key words : Astacida, China, crayfish, palaeobiogeography

Introduction

Members of the decapod Infraorder Astacidea, commonly referred to in English by the vernacular term 'crayfish', are also known by many other common names worldwide : crawfish, paper-shell crabs, ecrevisse, yabbies, mud-bugs, flusskrebs, rak, ditch bugs and koonac are just some of these names. With over 500 species currently known, which occur indigenously in tremendous numbers on all continents with the exception of Africa, this is perhaps not surprising (Adegboye, 1981 ; Hobbs, 1988 ; Pitre, 1993).

The evolutionary history of the Superfamily Astacoidea is currently the subject of some debate. The more traditional perspective, as suggested originally by Ortmann (1902, 1905), is that the crayfish as we know them today originated in a benthic marine environment similar to that occupied by the marine lobsters. From this ancestral stock emerged three major lines : the extinct Erymidae ; the relatively conservative Nephropidae (ancestors of the modern true lobsters) ; and the highly varied and widely dispersed Astacoidea and Parastacoidea, the 'true crayfishes', which then moved into the freshwaters of Laurasia and Gondwana as the result of two separate invasions.

A more recent perspective, however, is that of Scholtz (1995) and Scholtz and Richter (1995), in which the freshwater crayfishes are more closely related to the Thalassinida and Meiura (Brachyura and Anomala) than to the Homarida (forming a monophyletic group they refer to as the Fractosternalia). They suggested that the worldwide distribution of freshwater crayfish is the result of a single invasion into freshwater during the Triassic onto the 'supercontinent' Pangaea, which then diversified into the groups Parastacoidea (in Gondwana) and Astacoidea (in Laurasia) with the Late Mesozoic break-up of Pangaea.

Despite their relatively long geologic history, the fossil record for the crayfish is not very well understood. Many of the recent references to fossil crayfish originate from the research group of Rodney Feldmann, including the description of new taxa and/or redescription of previously described taxa (Feldmann, 1994 ; Feldmann *et al*., 1981) as well as such oddities as evidence of crayfish predation (Feldmann and May, 1991). Other sources of information on the palaeontological record for the Astacida include Rathbun (1926), van Straelen (1928a), Albrecht (1982, 1983) and Cope (1871). Much work has been done with respect to the global distribution patterns of the living Astacidea (e.g., Hobbs, 1988 ; Huxley, 1884 ; Ortmann, 1902), stemming largely from their wide use as an aquaculture crop ; however, relatively

little has been done with respect to a comprehensive analysis of the fossil members of this group beyond strict taxonomy.

Among the more intriguing of fossil astacidans has been material from the Late Mesozoic of China. We will here build on the original works of van Straelen (1928b) and Imaizumi (1938) and their respective description of two species of fossil freshwater crayfish, *Astacus licenti* and *A. spinirostrius*, from the Upper Jurassic (Jehol Group) of Liaoning Province, north-east China. This reassessment is prompted by the discovery of several new, well-preserved specimens from the region.

Collection localities

New material described in this paper was obtained from outcrops in Dawangzhangzi and Daxinfazi villages, Ling-yuan County, Liaoning Province, probably belonging to the Yixian Formation of the Upper Jurassic Jehol Group (Figure 1). While the general collection regions are known, their actual locations are vague because local farmers, who sell the specimens they collect to visiting academics, refuse to reveal their exact locations (one of which has actually been buried by the Chinese government to avoid poaching!). Enough is known of the geology of the region, however, to allow determination of the formations from which they have been collected.

Systematic Paleontology

Order Decapoda
Infraorder Astacida
Superfamily Astacoidea
Family Cambaridae
Subfamily Cambarinae
Genus ***Palaeocambarus*** gen. nov.

Type species.—*Astacus licenti* van Straelen, 1928b

Diagnosis.—Entire dorsal surface of cuticle covered with fine granulations. Rostrum with basal lateral spines. Elongate, bladelike scaphocerite. Chela of first pereiopod long and narrow with extensive pitting and spination. No hooks visible on ischia. Pleura large and rounded on abdominal segments 2–5, 2nd pleuron being largest. Pleopods elon-

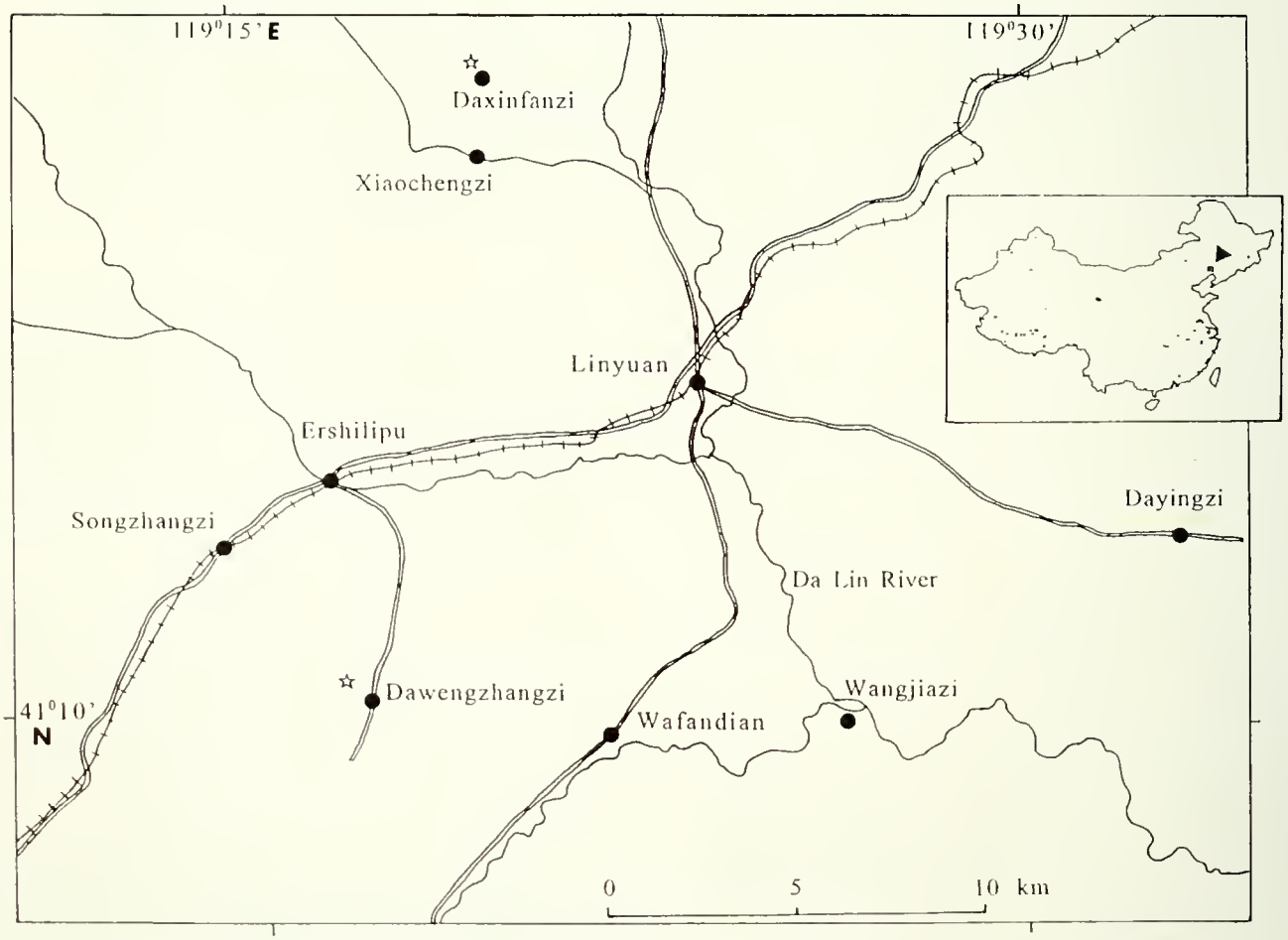

Figure 1. Locality map showing fossil crayfish collection localities near Daxinfanzi and Dawengzhangzi (stars).

gate and blade-like, with no specialization on first. Telson subrectangular with pair of large lateral spines and rounded distal margin.

Etymology.—The name of the genus is formed from 'palaeo', meaning 'ancient', in combination with '*Cambarus*', reflecting the new placement of its sole retained species in the Family Cambaridae.

Palaeocambarus licenti (van Straelen), 1928b

Figures 2, 4–6

Astacus licenti Van Straelen, 1928b, p. 133–135, figs. 1, 2 ; Imaizumi, 1938, p. 176, pl. 23, figs. 1, 2, 4, 5, 6, 11 ; Hamada and Itoigawa, 1983, p. 74, Pl. 3, fig. 6 ; Hobbs, 1988, p. 73.

Astacus spinirostrius Imaizumi, 1938, p. 176–177, pl. 23, figs. 9, 10, 12, 13, pl. 22, fig. 1 ; Hobbs, 1988, p. 73.

Diagnosis.—As for genus.

Emendation to Description.—Rostrum elongate and triangular with smooth margins. Approximately twice as long as wide at base (largest observed being 15 mm long and 7 mm wide at base). Length roughly one-third that of cephalothorax. A pair of anteriorly directed spines near base of rostrum that extend to approximately one-third rostrum's length (NIGP 126338). One specimen (NIGP 126342) shows two rows of small tubercles on ventral surface of rostrum. A single specimen (NIGP 126338) possesses small mid-dorsal spine at base of rostrum (Figures 4b, 4c).

Carapace developed, covers thorax completely. It extends partially over first pleomere mid-dorsally and completely so laterally due to slight postero-lateral enlargement (Figures 5a, 6a) ; simply decorated, possessing only a sinusoidal cervical groove (concave medially, curved convexly mid-laterally, concave again at lateral carapace margin) as well as a pair of short branchiocardic grooves that extend posteriorly from medial cervical groove (NIGP 126353, 126338 : Figure 4c). A single specimen (NIGP 126338) possesses a pair of well-developed gastric spines (Figure 4c). A slight ridge along lateral and posterior edges, but not evident along anterior margin. Optic notch well developed ; adjacent anterolateral margin gently rounded (Figure 6a). Entire carapace surface with granulated texture, several small spines/protrusions situated near cervical groove and around anterolateral region of carapace (NIGP 126338, 126353).

Antennules biflagellate, with medial flagellum larger than lateral flagellum. Peduncle not fully preserved on any specimens, although several specimens possess some peduncular segments. NIGP 126338 shows distal segment only, which is subrectangular in shape, slightly longer than wide, has rounded edges and is very small (less than 1 cm^2). NIGP 126346 with two distalmost segments, in shape with rounded edges and similar size dimensions. Middle segment noticeably more square than distalmost segment but equal in size. Distalmost segment similar in shape to others mentioned but with slight anterior projection on outer margin, possibly remains of small spine. Second segment approximately twice as wide as distal segment, suggesting it may be portion of basal segment, which is typically considerably larger than the other two antennular peduncle segments in recent crayfish. Antennular flagellae exceed 10 cm in length (Figures 4b, c, 5a, 6a).

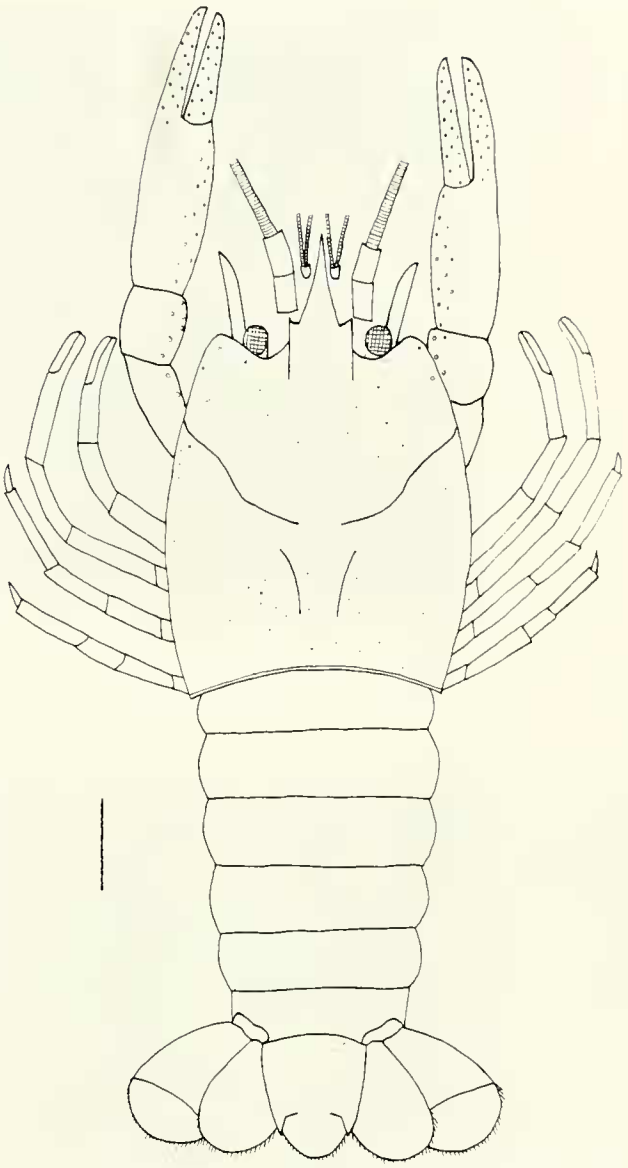

Figure 2. A reconstruction of *Palaeocambarus licenti* in dorsal view. Scale bar equals 1 cm.

Antennae each possess a single flagellum that is considerably longer than those of antennules (NIGP 126339 possesses a flagellum ~60 mm long, almost equal to total body length). Distal segments of peduncle relatively clear, but proximal peduncle arrangement difficult to interpret due to their frequently being overlapped by other structures such as antennal scales or rostrum. Distalmost segment rectangular in shape with concave proximal margin, long axis along length of antennae, and shows dimensions of approximately 3 mm width by 4 mm length. Adjacent segment similar in

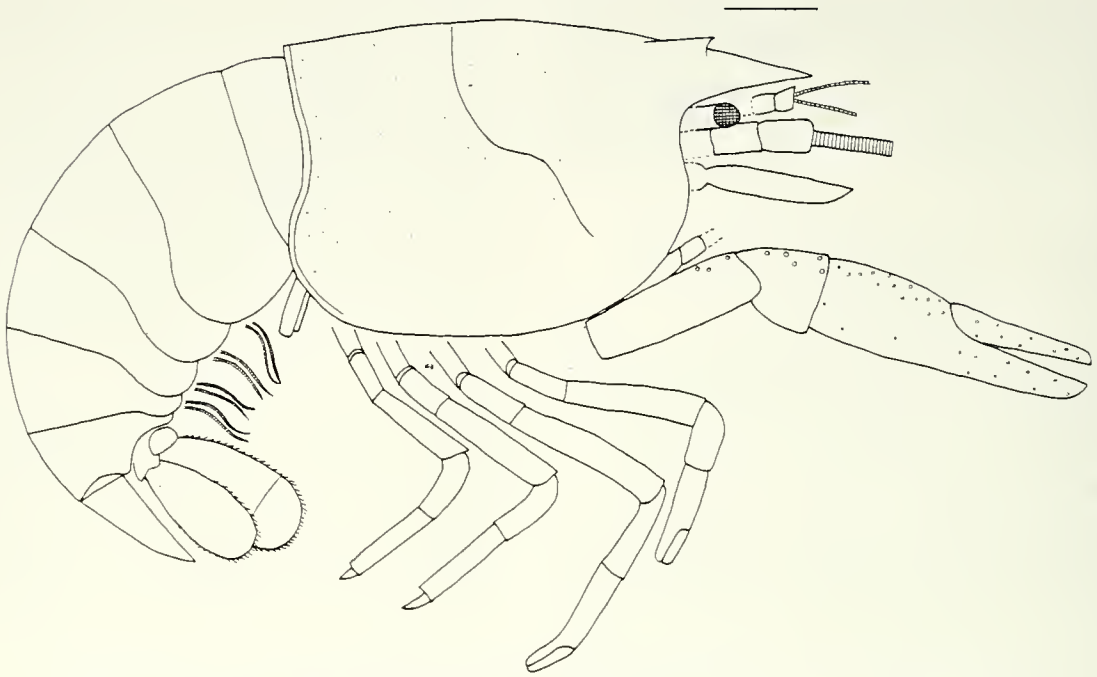

Figure 3. A reconstruction of *Cricoidoscelosus aethus* in lateral view. Scale bar equals 1 cm.

shape and size but lacks curved proximal edge. Middle segment rectangular in shape and similar in length to two distalmost segments, approximately 2/3 as wide as long; attached laterally to basis, which is short (approximately 2 mm) and wide (4 mm) and possesses an arcuate proximal margin. Coxa rectangular in shape with slightly convexly curved posterior margin, slightly less wide than basis and possesses medial anterior projection, which 'fills' the posterior groove in basis (NIGP 126338; Figures 4c, 6a).

Well-developed, blade-shaped scaphocerites extend from lateral half of each antennal basis. They reach maximum length of 15 mm, are setose along lateral margins (only setal bases, not setae themselves, preserved). One specimen (NIGP 126343) possesses small, medially directed process at anterior end of scaphocerite (Figures 4a, 4c, 5a, 6a).

Eyes located near base of scaphocerites, always somewhat deformed but were probably round or slightly ovoid and approximately 2 mm wide. They were probably closely associated with body, with short eyestalks of 1-2 mm, are always found superimposed over rostrum and/or antennal peduncle (i.e., NIGP 126342).

Prominent epistome, close to 10 mm in width, visible on ventrally preserved specimens suggesting it was heavily sclerotized in life (as seen with recent crayfish). It possesses an arched v-like shape and is directed anteriorly. Medial process present near the anterior end, with two small longitudinally arranged pits. Anteriormost end possesses forward-directed process, approximately one-quarter width of labrum and trapezoidal in shape, wider edge anteriormost (NIGP 126342: Figure 6c).

Some dorsoventrally oriented specimens show details of well-developed gastric mill, triangular in shape, directed posteriorly and found immediately behind labrum (NIGP 126342); made up of two sets of very small, serially arranged peg-like teeth in slightly inwardly curved rows, approximately 16 teeth per element. No median tooth present. Moulds of paired circular gastroliths, up to 7 mm in width, prominent in several specimens: in NIGP 126338 and 126353, one has rounded convex surface while other possesses an outer depressed ridge with raised circular region (Figures 4c, 5a, 6c).

Elements of first and second maxillipedes preserved on some specimens; however, they are impossible to interpret with any certainty due to being damaged and/or obscured by anterior structures such as carapace, 3rd maxillipede and 1st thoracomere. Third maxillipede possesses large ischium, up to 10 mm in length and 3 mm in width. Extensive crista dentata found along ischial inner margin. Merus is small, approximately 2 mm long and 4 mm wide and ovoid in shape. Carpus slightly less in width than merus and is rectangular in shape. Propodus rectangular in shape and approximately 2 mm by 4 mm. Dactyl slightly smaller than preceding segments, approximately 1.5 mm by 3 mm, and elongate with pointed distal end (NIGP 126338; Figures 4b, 6a).

Pereiopods 1 to 5 large and well developed. Pereiopod 1 considerably larger than others, propodus and dactylus modified to form large claw (heavily decorated with spines and pits, especially medially), may exceed 40 mm in total length. Carpus reaches maximum length of approximately 10 mm, is rectangular (almost square in some specimens) in shape and usually narrows slightly at proximal end. Merus

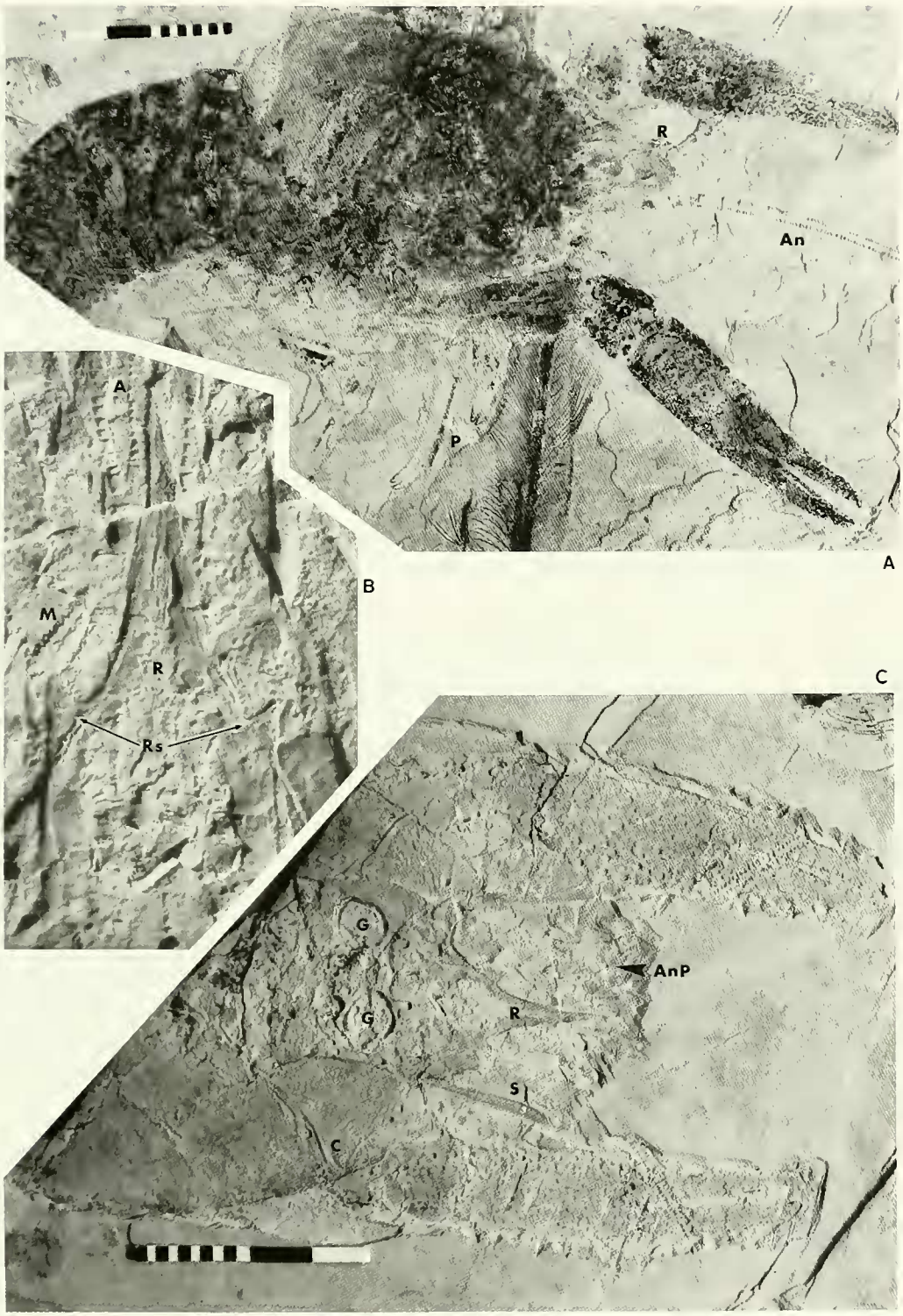

Figure 4. **A.** Lateral view of incomplete specimen (NIGP 126339) of *Palaeocambarus licenti* (with Lycopteran fish) (An = antenna, P = pereiopods, R = rostrum). Scale bar = 2 cm. **B.** Close up of rostrum, distal end of 3rd maxillipede and antennules of specimen of *P. licenti* (NIGP 126338) (A = antennule, M = third maxillipede, R = rostrum, Rs = rostral spine) ×5.4. **C.** Anterior end of incomplete specimen of *P. licenti* (NIGP 126338) (AnP = antennal peduncle, C = cervical groove, G = gastrolith, R = rostrum, S = scaphocerite). Scale bar = 2 cm.

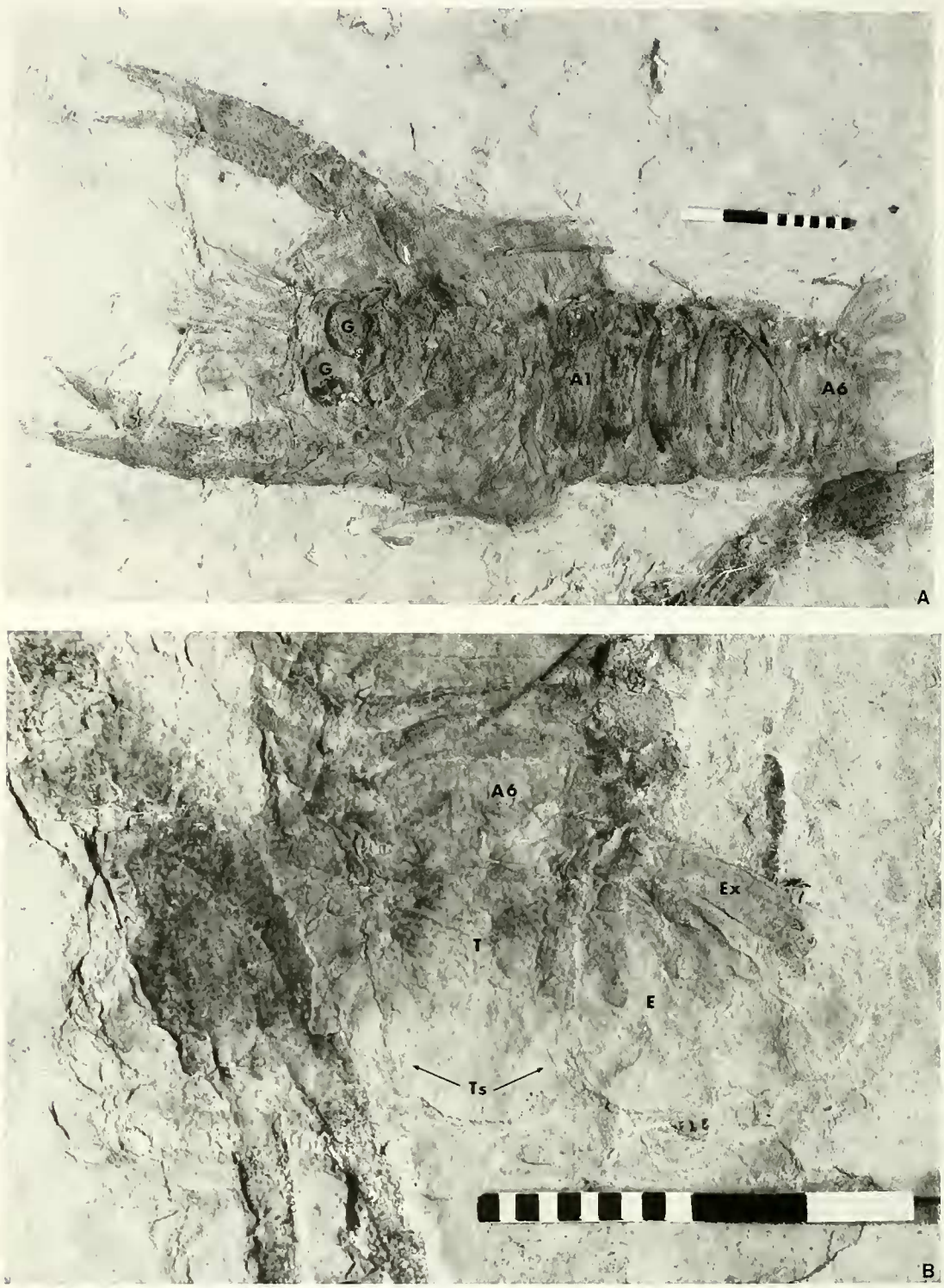

Figure 5. **A.** dorsal view of complete specimen (NIGP 126353) of *Palaeocambarus licenti* (with incomplete chelipede from another specimen) (A1 = first abdominal segment, A6 = sixth abdominal segment, G = gastrolith). Scale bar = 2 cm. **B.** close-up of tailfan of the same specimen (A6 = sixth abdominal segment, E = uropodal endopod, Ex = uropodal exopod, T = telson, Ts = telson spines). Scale bar = 2 cm.

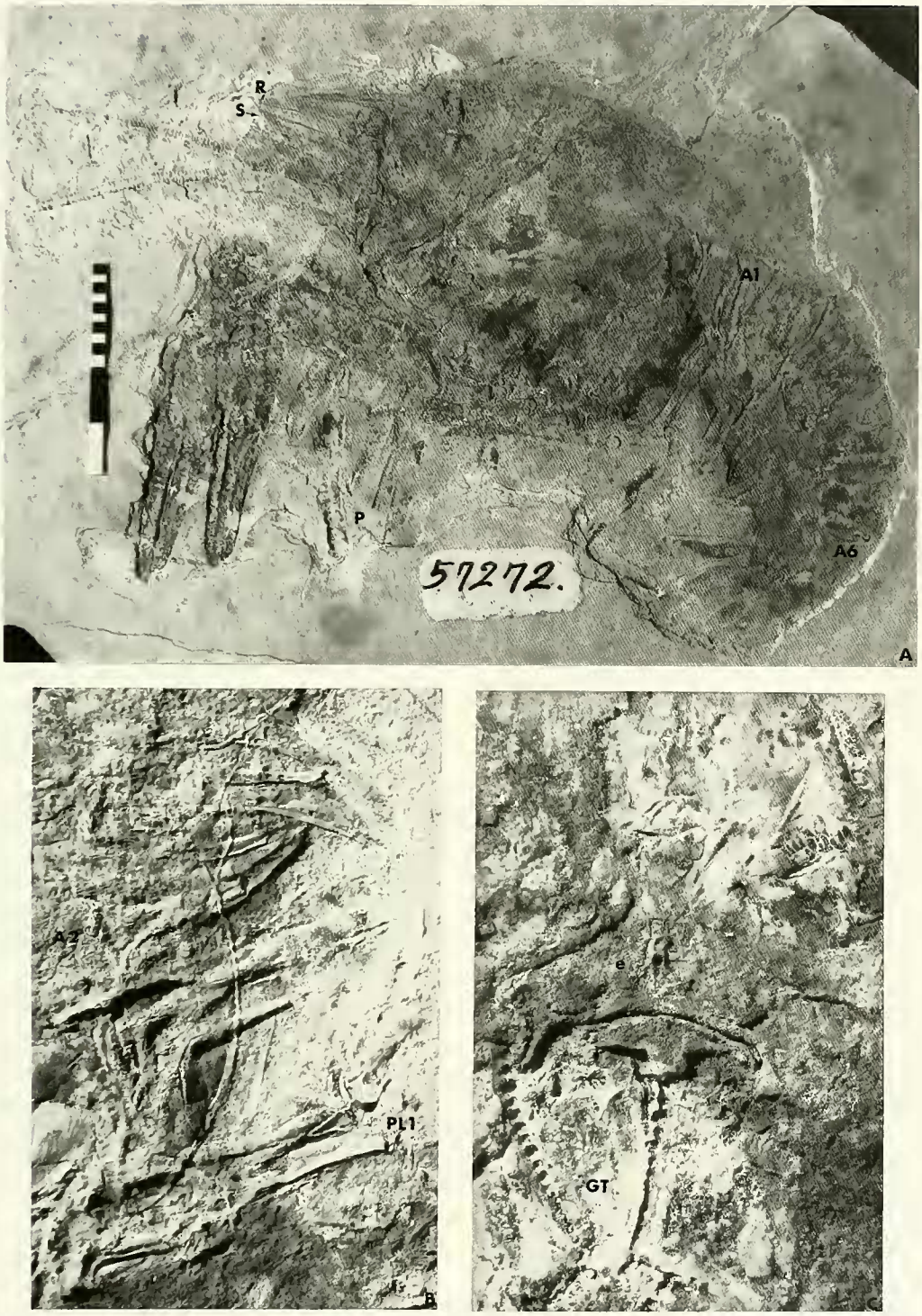

Figure 6. **A.** Specimen of *P. licenti* from Imaizumi's material (="*Astacus spinirostrius*": IGP 57272) (A1=first abdominal segment, A6=sixth abdominal segment, P=pereiopods, R=rostrum, S=scaphocerite). Scale bar=2 cm. **B.** Close-up of pleopods of IGP 57272, anterior to bottom (A2=second abdominal segment, PL1=first pleopod). ×5.0. **C.** Ventral view of anterior end of specimen of *P. licenti* (NIGP 126342) (e=epistome, GT=gastric teeth). ×6.4.

is elongate and approximately one-half the length of propodus (up to 7-8 mm); is rectangular in lateral view but triangular in dorsal view, by far the most common style of preservation seen in this material. Dactylus, propodus, carpus and merus decorated with large spine-like processes, most commonly so on dactyl and propodus. Those on carpus and merus largest, reaching almost 1 mm in width at base (NIGP 126338). Ischium is small and roughly square in shape, showing no sign of hooks. Basis triangular in shape, with rounded proximal margin where it comes into contact with rectangular coxa (NIGP 126339; Figures 4a, 5a, 6a).

Pereiopods 2 to 5 considerably smaller than pereiopod 1, developed as walking legs (as opposed to the chela of pereiopod 1). Coxa possesses lateral distal groove to accommodate basis, is slightly longer than basis (NIGP 126339, 126346). Basis concave distally, forming a groove where it contacts ischium, but is rounded proximally and slightly wider at its distal than proximal end. Ischium short (approximately 0.4 cm) and tapered slightly where it connects with basis. Merus elongate (approx. 1.5-2.0 cm) while carpus considerably shorter (approx. 0.5 cm) and acts as 'knee joint' (NIGP 126339, 126354). In pereiopods 2 and 3, elongate (approx. 1.5 cm) propodus acts with dactylus to form small chelipede at distal end of pereiopod, much smaller than those of 1st pereiopods (NIGP 126339) (Figures 4a, 6a).

Abdomen elongate and rectangular in dorsal view, narrowing slightly distally. Segment length consistent over first 4 segments with largest specimen seen (NIGP 126353) showing lengths of 0.6 mm. Fifth and sixth segments somewhat shorter with lengths of 0.5 and 0.45 mm, respectively (Figure 5a). Pleura rounded and well-developed on tergites 2-5, 2nd expanded slightly posteriorly and thus larger than others. No pleurae seen on tergite 1, pleurae on tergite 6 greatly reduced to accommodate uropods. Sternites reduced in width distally, but sternite/tergite size ratio (sternites being approximately 70 percent as wide as tergites) remains fairly consistent along abdomen. Sternal bars 'bar-belled' in shape, narrow medially but several times wider distally; this results in ovoid gaps, pointed laterally, where arthrodial membranes would have been located in life (NIGP 126353, 126346; Figure 5a).

Circular/ovoid scars evident near antero-lateral regions of sternites. Pleopods elongate, blade-like in shape. There is no evidence of styliform first pleopod in material collected for this study (but see Discussion).

Tailfan very well developed (Figure 5b). Telson large and subrectangular with slightly convex anterior margin. Tapers distally, possesses straight lateral margins, with well-rounded setose distal margin, which is delineated by complete transverse suture. A pair of posteriorly directed spines located just posterior to transverse suture. Uropods are also large, with exopod slightly longer than endopod. Exopod possesses diaresis, is setose along its rounded distal end and along posteriormost portion of lateral margin. Endopod also setose along distal margin (NIGP 126346, 126353).

Etymology.—Van Straelen's specific epithet *licenti* is retained.

Measurements.—Measurements (in mm) are given in Table 1.

Types.—Van Straelen (1928b) indicated his 'nearly complete' specimen in Pl. 1, Figure 1 as the type specimen for *A. licenti*. His material was housed at Hoang Ho Pai Ho Museum, Tientsin, China. Imaizumi's (1938) material (Reg. Nos. 57254, 57267, 57271, 57272 and 57274) is stored in the Institute of Geology and Palaeontology (abbreviated here as IGP), Tohoku University, Sendai, Japan.

Material examined.—New material used in this study includes NIGP (Nanjing Institute of Geology and Palaeontology) 126338-126339, 126341-4 and 126346-126354. Several other uncatalogued specimens are currently in the NIGP collections, some of which were photographed for use in this study (owing to the difficulty in transporting the large slabs upon which these specimens are found or the inferior quality of preservation of several of these specimens). Specimens 57254, 57267 and 57272 from the Institute of Geology and Palaeontology, Tohoku University, Sendai, Japan were also used in this study.

Occurrences.—The material used in the original description of *Astacus licenti* was collected from an unspecified locality, representing Upper Jurassic *Lycoptera/Ephemeropsis* shales, south-west of Shenyang City, Liaoning Province, China. *Astacus spinirostrius* was described from material collected from equivalent *Lycoptera* beds in Lingyuan County, Liaoning. The newest material was collected from beds believed to be of equivalent age in Daxinfanzi and Dawangzhangzi villages, Lingyuan County. This locality cannot be described with any greater detail, as these (as well as other) specimens were bought by the Nanjing Institute of Geology and Palaeontology from local farmers, who refused to divulge the exact locations.

Remarks.—The gastric teeth found in this taxon are atypical when compared to those of other crayfish and other decapods in general. Icely and Nott (1992) and Felgenhauer and Abele (1989) have described in considerable detail the foregut morphology as found in various decapod taxa. The physical make-up of the decapod foregut and the gastric mill in particular are particularly complex systems, made up of up to 60 ossicles of varying size and shape. While we are unable to determine the nature of these ossicles in our fossils, we are able to see evidence of the gastric mill elements. It would probably be best described as 'relatively primitive', based on the classification scheme provided by Felgenhauer and Abele (1989). In their 3-tiered system, the most primitive 'type I' foregut possesses heavily sclerotized lateral teeth that work in association with the median tooth to filter and/or masticate food. In their 'type II' foregut, the gastric mill is "completely absent": the median tooth is never present, while the lateral teeth may be replaced by setose lateral ridges. The gastric mill found in *P. licenti* appears to be an intermediate between these two forms: it possesses no medial tooth, but the paired lateral teeth are present and well developed.

However, the system suggested by Felgenhauer and Abele (1989) is derived from studies of the 'lower Decapoda' (including the suborders Dendrobranchiata and Pleocyemata). Recent crayfish are known to possess both a single medial and paired lateral gastric teeth (e.g., Holdich and Reeve, 1988). Thus, what we see with our material is a situation

Table 1. Morphological measurements (in mm) for *P. licenti* and *C. aethus*.

specimen[2]	cephalothorax length	rostrum length	rostrum width	abdomen length	abdomen width	left exopod length	left exopod width	right exopod length	right exopod width	left endopod length	left endopod width	right endopod length	right endopod width	telson length	telson width	left chelipede length	left chelipede width	right chelipede length	right chelipede width	left chelipede propodus length	right chelipede propodus length
P. licenti																					
126338		13	17													31.5	8.5	30	8	15	15
126339	38	13														35	9	35	9	18	18
126341																12	3	12	3		
126342	33	10	3.5													25	7.5	24	7		12
126343		15	7															45	11		23
126344	17	6.5						6	2.5	25		4.5	2.5	4.5			3.5		3.5		
126346	26	10	5	29.5		10	6	10	6		5		4.5	8	9	22	6.5	23	6.5	13	12
126353	31	11		35	23	13		12.5	8.5			10.5	7	12	10.5	27	6.5	28	7.5	13	14
57254	35	11	5	35	26	13	5	14	6	10	5	11	5	13	12	38	11	38	10	13	14
57267				24																	
57272	33	12	4.9													23	6	24	6	14	13
RT129	33	10		35.5	23			13	9			11	7.5	12	10	27	6.5		7	14	
RT130																28	7.5	29		15	14.5
RT131	44	10		33												35	10	37	10	15	18
RT132				16	11																
RT133	29	11.5		32												33	9			17	
RT134																		32	8.5		12
RT138	28	10														23	5.5	23	5	13	12
RT141								12.5	9.5			12.5	9		10.5	17	5			7.5	
RT143	30	10	6	31														23	6.5		12
RT146	21			24.5	16										7.5	16	4.5	17	5	7.5	8.5
RT150	17.5	4.5		23.5																	
C. aethus																					
126337	34	9	3										3.5	8	10	25	8	27.5	8	13	13
126340	22	7		30				7.5						5		13.5		14.5	4	8	7
126345				24				12	8.5			10	6.5	11.5	10						

possibly reflecting an intermediate state between the three-toothed array seen in recent crayfish and the reduced system seen in many of the 'lower' Decapoda.

Family Cricoidoscelosidae fam. nov.

Type Genus.—*Cricoidoscelosus* gen. nov.

Diagnosis.—Rostrum with rounded base and lateral spines. Bladelike scaphocerite. Well-developed first chelae. No ischial hooks on pereiopods. Rounded pleurae. First pleopod styliform in males, remainder annulate. Large telson with large lateral spines.

Etymology.—The name of this family is derived from the Greek words 'cricoides' (meaning 'annular') and 'scelos' (meaning 'leg').

Cricoidoscelosus gen. nov.

Type species.—*Cricoidoscelosus aethus* sp. nov.

Diagnosis.—Rostrum with rounded base and curved lateral spines. Scaphocerite long, bladelike. Chela of first pereiopod well developed, highly nodose. No ischial hooks evident. Rounded pleura on abdominal segments 2–5, the 2nd being the largest. Pleopods annulate, with the first specialized as styliform copulatory appendages in males. Female with paired circular 'pores' on 3rd abdominal sternite. Telson with large lateral spines and rounded distal margin.

Etymology.—Same as for the family.

Cricoidoscelosus aethus sp. nov.

Figures 3, 7–8

Diagnosis.—Same as for genus.

Description.—Rostrum elongate, approximately 9 mm in length, narrow and triangular along its anterior two-thirds; posterior third roughly circular in shape. Pair of short, curved spines projects anterolaterally from anterior end of basal portion of rostrum (NIGP 126337 : Figure 7a, b).

Carapace heavily sclerotized, covers thorax completely and partially covers first abdominal segment dorsally, almost completely covers first abdominal segment ventrolaterally due to enlargement (NIGP 126340). Sinusoidal cervical groove present, no other carapace grooves visible. Slight ridge visible along carapace dorsal and lateral margin. Optic notch well developed. Surface of carapace granulate with small spines near anteriormost end of carapace.

Antennules are biflagellate, medial flagellum slightly longer than outer flagellum. Peduncles not completely preserved on any specimens: two distalmost peduncular segments rectangular, approximately 1.5 mm by 1.5 mm. Other peduncular segments are unclear (NIGP 126337, 126340).

Antennae each with single elongate flagellum, longest seen 5.1 cm in length (NIGP 126337). No specimens with complete antennal peduncules, but some segments are preserved. Distalmost segment rectangular in shape, approximately 4 mm^2, with proximal margin concave. Adjacent segment similar in shape and size but with lateral side extended to approximately 5 mm long. Proximalmost segment rectangular and elongate, approximately 4 mm wide and 2 mm long. Coxa and basis unclear. Antennal gland present. Scaphocerites elongate, up to 10 mm in length: outer margin straight, inner margin slightly curved. Setal bases present along outer margin (NIGP 126337). Eyes present but not preserved intact: remains found lateral to base of scaphocerites. No peduncle preserved (NIGP 126337).

Epistome v-shaped and directed anteriorly, with anterior process as described for *P. licenti*. However, medial process possesses no pits and is anteriorly directed (NIGP 126337). Gastric structures not evident.

3rd maxillipede well developed, reaching anteriorly to antennal peduncles. Ischium large, 8 mm in length and 3 mm in width, with cristata dentata along inner margin. Merus ovoid, 2 mm wide and 4 mm long. Remaining elements unclear (NIGP 126337).

Pereiopod 1 with propodus and dactylus modified to form large claw (up to 25 mm long), decorated with spines and pits distally and medially. Carpus rectangular in shape, up to 7 mm wide and 5 mm long. Merus large and elongate, exceeding 10 mm. Ischium square, lacking hooks. Basis triangular, gently rounded at contact with rectangular coxa (NIGP 126337, 126355).

Pereiopods 2 to 5 reduced, developed as walking legs with small distal chelae on 2–3 formed from dactyl and propodus. Coxa slightly longer than basis, 2–3 mm in length. Basis with concave interface with ischium, which is approximately 5 mm long and slightly broader distally. Merus rectangular, may exceed 10 mm in length; carpus also elongate and rectangular, up to 10 mm in length (NIGP 126337, 126355).

Abdomen elongate and rectangular, slightly wider at its anterior. Segment length regular for first 4 segments, with last two slightly shorter in length. Abdominal pleura well developed, posterolaterally oriented. Pleurae absent on tergite 1, reduced on tergite 6 to accommodate uropods. Sternites developed across tergite ventral surface, pointed laterally (NIGP 126337, 126345, 126355).

Pleopod 1 visible in one laterally oriented specimen (NIGP 126355), developed as elongate, styliform appendage, probably utilized as a copulatory structure (as in Astacidae and Cambaridae). Distalmost portion only preserved: approximately 10 mm in length and 3 mm wide at base, tapering to slightly less than 2 mm wide distally. It is simple and undecorated (Figures 8a–b).

Telson large and subrectangular with convex anterior margin; tapers distally, has rounded setose distal margin with complete transverse suture. Pair of posteriorly directed spines adjacent to transverse suture, one on either side of telson. Uropods large, exopod slightly longer than endopod. Exopod and endopod with setose distal margins; exopod also with setose posterolateral margin and diaresis (NIGP 126337, 126345).

Etymology.—The species name is derived from the Greek word 'aethus' (meaning 'unusual').

Type.—Holotype NIGP 126337, paratype NIGP 126355; housed at the Nanjing Institute of Geology and Palaeontology, Academia Sinica, Nanjing, the People's

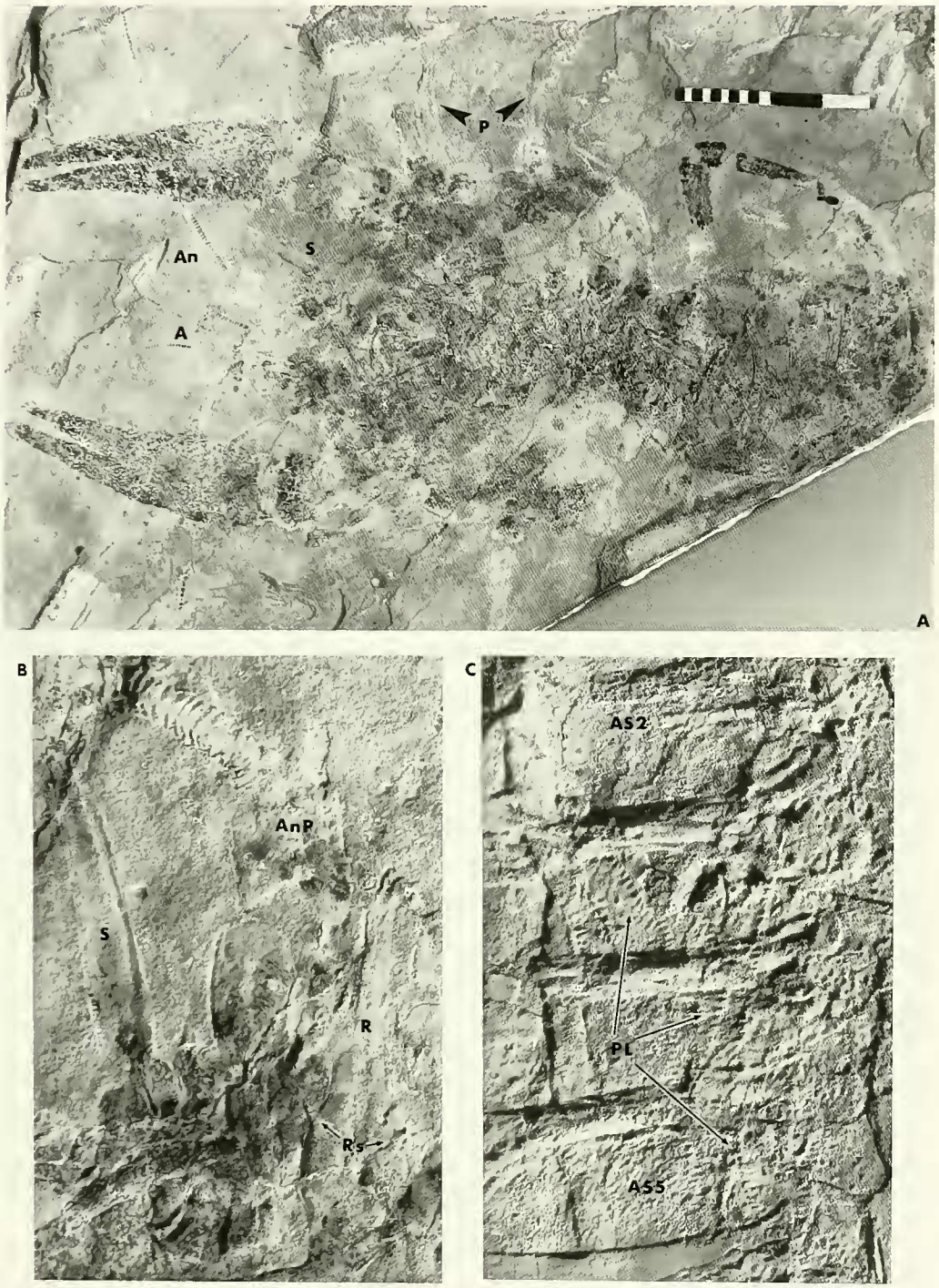

Figure 7. **A.** Ventral view of *Cricoidoscelosus aethus* holotype (NIGP 126337) (A = antennules, An = antenna, P = pereiopods, S = scaphocerite). Scale bar = 2 cm. **B.** Close-up of ventral view of *C. aethus* (NIGP 126337) (AnP = antennal peduncle, R = rostrum, Rs = rostral spines, S = scaphocerite). ×4.9. **C.** Close-up of ventral view of abdomen with pleopods of specimen of *C. aethus* (NIGP 126345) (AS2 = abdominal sternite 2, AS5 = abdominal sternite 5, PL = pleopods). ×5.4.

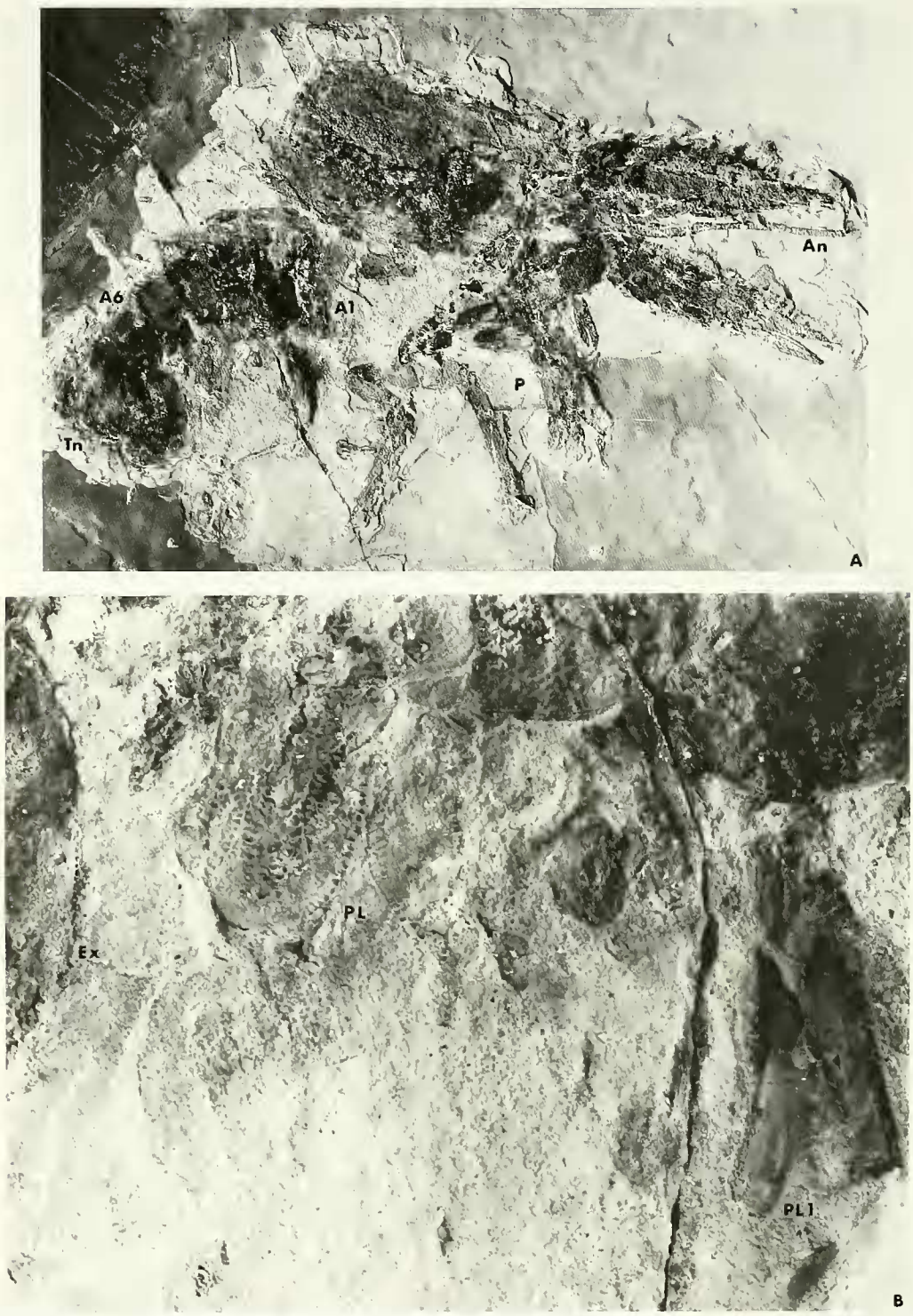

Figure 8. **A.** Lateral view of *Cricoidoscelosus aethus* paratype (NIGP 126355) (A1 = first abdominal segment, A6 = sixth abdominal segment, An = antenna, P = pereiopods, Tn = tailfan. ×0.64. **B.** Close-up of pleopods of the same specimen (PL = pleopods, PL1 = first pleopod, Ex = uropodal exopod). ×4.1.

Republic of China.

Material examined.—NIGP 126337, 126340, 126345, 126355.

Remarks.—Few specimens exist that can definitively be placed in this taxon from the several specimens in our collections. There is no doubt as to its distinct nature, however, due to its highly characteristic and unique pleopods that are fortunately preserved in several orientations.

Discussion.—A reconstruction of *P. licenti* is provided in Figure 2 while *C. aethus* is shown reconstructed in Figure 3.

Astacus licenti was first described by van Straelen (1928b), based on 3 specimens collected from an unspecified "point south-west of Moukden, in Eastern Mongolia" (actually in north-east Liaoning Province, People's Republic of China). In this description, his assignment of this new species to the genus *Astacus* was "provisional... in the most extensive sense of the genus" (he felt, however, that it belonged "undoubtedly to the family of the Astacidae") (van Straelen, 1928b).

Imaizumi (1938) described a second species, *Astacus spinirostrius*, based on two new specimens collected from equivalent *Lycoptera davidii* beds from Niehhutzekow, near Lingyuan, China (three specimens of *A. licenti* were also collected at the same time from the region). In his paper, he discussed how both *A. licenti* and *A. spinirostrius* are in fact more similar ("particularly in the long slender chelipede and the rounded-off pleural plate") to the fossil form *Pseudoastacus* than to the recent *Cambaroides* [then *Astacus* (*Cambaroides*)] species in Asia (Imaizumi, 1938). Apparently there was, in the minds of both van Straelen and Imaizumi, considerable question as to the definitive generic assignments of these new fossil taxa.

Hobbs (1988) discussed how the chelipedes of *A. licenti* are in fact more similar to the eastern American cambarid genus *Procambarus* than to either *Astacus* or *Cambaroides*; he also suggested that the chelae and the abdominal pleurae of *A. licenti* more closely resemble those of the primitive cambarine genus *Procambarus* than either of the Eurasian genera. These issues, coupled with the discrepancies between the early descriptions and the nature of the fossils examined for this study, were keys that forced us to rethink the taxonomic affinities of this species.

Unfortunately, the key characters used to separate the Astacidae from the Cambaridae (Hobbs, 1974, 1989) are impossible to observe from our material. For example, cyclic dimorphism (present in the Cambaridae, absent in the Astacidae) is impossible to identify in these fossils; and the detailed nature of the 1st pleopod (subtubular distally and lacking ornamentation in the Astacidae, with shallow groove or deep sperm groove and with terminal ornamentation in the Cambaridae) is also not evident in the specimens described here. Our decision to move this taxon from the Family Astacidae to the Family Cambaridae is, then, based on less specific features, such as the absence of astacid crayfish from (and presence of cambarid genera in) the Asian region. The shape of the chelae is another feature mentioned by previous authors (Imaizumi, 1938; Faxon, 1885) as suggesting alternative relationships for *P. licenti*: it has been compared to the chelae of the extinct *Pseudastacus* and to the recent genus *Procambarus*, presumed to be the most 'primitive' of the cambarid genera (Hobbs, 1988). While we can give no definitive answer to the question of what *P. licenti* may be most closely related to, we feel that these points warrant the movement of this species from the Family Astacidae to the Family Cambaridae.

After examining the original plates of van Straelen (1928b) and Imaizumi (1938) and some of Imaizumi's original material (IGP specimens 57272, 57254 and 57267, Tohoku University, Japan), we determined that several of the features proposed by Imaizumi as distinguishing characters between *A. licenti* and *A. spinirostrius* are in fact artifacts of preservation. For example, his 'spines on the mid-dorsal line' of the rostrum appear to be the pair of lateral spines found near the base of the rostrum but viewed from a slightly skewed angle, giving them the appearance of projecting from the middle of the rostrum. These spines are clearly located on the posterolateral region of the rostrum when dorsally preserved specimens are examined, something Imaizumi lacked. The same is true for such features as the shape of the pleural plates and the relative lengths of the exo- and endopods of the uropods: these features appear to lose their usefulness in defining separate taxa when several specimens preserved in multiple orientations are examined.

Imaizumi (1938) also suggested the presence of gastric spines as being a characteristic of *A. licenti* not shared with *A. spinirostrius*. This question of the presence/absence of a pair of gastric spines is one that must be addressed here, for several reasons. First, no gastric spines were noted with re-examination of the material described by Imaizumi, removing this character as a potential feature in distinguishing between the previously established taxa from this region. Secondly, a single specimen of the new material examined does possess a set of well-developed, anteriorly directed gastric spines (closely associated with several smaller spines and processes). This specimen is, however, far from complete with only the 'head', anteriormost carapace and first pereiopods preserved; thus, it is impossible to compare it with the other specimens with respect to either abdominal or appendage characters. Gastric spines aside, this specimen is largely identical to the other specimens of *P. licenti* examined, suggesting that these gastric spines may not be a species-specific character. They may instead represent a sex-specific character, but this cannot be determined without a better understanding of other sex-specific differences within this species. Another possibility is that they may simply reflect a character that shows flexibility in expression and/or preservation and may vary from individual to individual within a species, as seen in the Palaeozoic pygocephalomorphs (Schram, 1979). Such features would seem to provide no taxonomic information for this material.

The question of sexual dimorphism is further complicated by the narrow range of morphological characters that exhibit a truly dimorphic state in the crayfish. Some dimorphic characters, such as the generally wider abdomen seen in females, are too general to be of any use in a study utilizing fossil specimens. Sexual dimorphism in the Cambaridae, for example, is characterized by several features: males exhibit

cyclic dimorphism with the presence of a sperm groove (and sometimes ornaments such as spines) on the distal portion of the first pleopod, while females possess a seminal receptacle between the 4th and 5th pereiopods. In addition, males possess hooks on at least one set of ischia. Sexual dimorphism in the Astacidae is characterized by a lack of cyclic dimorphism and an unornamented subtubular first pleopod in the males, while the females lack a seminal receptacle (Hobbs, 1988). Such features are difficult if not impossible to determine with fossil material.

Such dimorphic features, in general, present a problem with respect to our material. None of our specimens of *P. licenti* possesses a styliform first pleopod: whether this is due to its complete absence in this species, to our having no males in our material, or to this feature simply not being preserved is impossible to evaluate. None of our specimens appears to possess hooks on the ischia; this may be due to our relative lack of males, as suggested earlier, or to the fact that few of our specimens possess well-preserved pereiopods. It is possible that perhaps those that we possess are female and thus would have not possessed these ischial hooks.

However, two (IGP 57272, 57254) of the specimens presented by Imaizumi (1938) do possess a pair of styliform first pleopods, whose distalmost segments are unfortunately the only parts preserved. Those of IGP 57272 are preserved laterally and are elongate, slightly curved anteriorly and tapered distally, being 5 mm in length and 1 mm wide at their widest point (Figures 6a, b). IGP Specimen 57254 shows only one of the pair of first pleopods, preserved in ventral view. It is 7 mm long and 1 mm wide, and is slightly laterally directed proximally. No other pleopods are visible on this specimen. These styliform pleopods suggest that this species belongs to either the Cambaridae or the Astacidae (both characterized by the presence of a styliform first pleopod in the males; it is absent in the Parastacidae). We consider these specimens to be males of the species *P. licenti*, supporting again a cambarid/astacid taxonomic position for this genus. Pleopods 2-6 of IGP 57272 are more 'typical' crayfish pleopods, being elongate and blade-like, than the annulate pleopods possessed by *C. aethus*.

The distinct annulate pleopods (2-6) of *C. aethus* are, we feel, sufficiently different from those seen in any other crayfish to warrant placing them in their own family. The presence of styliform first pleopods, however, is an indication that this taxon is related in some degree to at least one (if not both) of the northern hemisphere astacoidean families, Astacidae and Cambaridae.

One phenomenon that is shared by specimens of both *C. aethus* (NIGP 126340) and *P. licenti* (NIGP 126338, 126346, 126353, 126354) is the presence of gastroliths. Those in *P. licenti* are preserved here as moulds of their actual state in recent animals (e.g., Lowrey, 1988), in which the ridged face is the attachment surface to the wall of the cardiac region of the foregut. This is presumed to be the natural state in our animals as well. These gastroliths are present in freshly molted animals and act as calcium storage packages to be reused in the recalcification of the exoskeleton after ecdysis. It is evident that our sample possesses both recently molted and fully calcified animals. This also is reflected in the general preservation of these animals, as most of the specimens with gastroliths appear to have been less heavily sclerotized than those without gastroliths.

Ortmann [1902; 1905 (summarized in Hobbs, 1988)] made the first attempt to interpret the history of origin, diversification and dispersal for the crayfish, in a synthesis that has remained largely unchallenged until just recently. He suggested that the ancestors of the Potamobiidae (=Astacoidea) and Parastacidae lived in Sino-Australia (and possibly Antarctica) in the Lower Cretaceous, with *Astacoides* reaching Madagascar during the Middle Cretaceous via a Lemurian land-bridge. The Upper Cretaceous saw the splitting of eastern Asia and Australia, resulting in the differentiation of the Potamobiidae in eastern Asia (and then into western North America and Mexico) and the Parastacidae in Australia and Antarctica. In the Lower Tertiary, the genus *Cambarus* arose from *Potamobius* in Mexico, which then spread through eastern North America; while the Parastacidae extended its range through much of South America and Australia, splitting into several genera in the process. During and since the Upper Tertiary, the Potamobiidae moved into western Asia and Europe, with the Parastacidae remaining in South America, Australia and New Zealand. Following Ortmann's reasoning, the ancestor to the crayfish that we recognize today is believed to have originated in a benthic environment similar to that occupied by the modern marine lobsters. From this ancestral stock, three major lines emerged: the extinct Erymidae; the relatively conservative Nephropidae (ancestors of the modern true lobsters); and the highly varied and widely dispersed Astacoidea and Parastacoidea, the true crayfishes.

More recently, however, Scholtz (1995) and Scholtz and Richter (1995) have proposed a closer relationship between the Astacida and the Thalassinida and Meiura than between the Astacida and Homarida. This suggestion is based on phylogenetic systematic studies and a far better understanding of the fossil record for this group. Their research suggests that many of the morphological similarities once cited as uniting the Astacida and the Homarida are in fact plesiomorphic characters, with no true synapomorphies joining these two taxa. Instead, their phylogenetic analysis revealed two characters that support their taxon Fractosternalia (including the Astacida, Thalassinida, Anomala and Brachyura): a movable last thoracic sternite and a pattern of calcified pleural parts connecting thorax and pleon. Scholtz (1995) further goes on to suggest that the invasion into freshwater by the astacoidean ancestor occurred during the Triassic on the "supercontinent" Pangaea. This ancestor then developed into the Parastacidae in the Southern Hemisphere and the Astacidae and Cambaridae in the Northern Hemisphere with the break-up of the Pangaea landmass into Amero-Eurasia and Gondwana.

Our fossil material, dating back to the Jurassic, confirms that crayfish did indeed move into freshwater considerably earlier than the time suggested by Ortmann. However, the features suggested by Scholtz and Richter (1995) as allying the Astacida with the Thalassinida instead of the Homarida are impossible to distinguish with the fossil material at hand.

It may perhaps be interesting to briefly comment on the rationales behind these two suggested evolutionary histories for the 'crayfish'. Ortmann's (1902, 1905) scheme was very much a product of his time, when distributions were believed by many [e.g., Darwin (1859, Chs. 12 and 13) and Wallace (1876 ; in Hallam, 1994)] to be strictly dispersalist in nature. By his reckoning, crayfish distributions enlarged slowly with the movement of these animals from one point to another and their subsequent establishment in these new territories. He explained problematic distributions, such as the appearance of crayfish on Madagascar, by the presumed presence of land bridges (in this case, a Lemurian land bridge). Scholtz's considerations, on the other hand, are a product of our modern understanding of how plate tectonics or continental drift (Wegener, 1924 ; in Hallam, 1994) and its association with vicariance biogeography (Croizat *et al.*, 1974) allow for the presence of closely related organisms in isolated localities via the movement of land masses towards and away from each other with time (Hallam, 1994).

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